7. On the Classification of the Palæozoic Echinoderms of the Group Ophiuroidea. By J. W. GREGORY, D.Sc., F.Z.S.

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For fifty years after Forbes, in 1840 [3. p. xiv], proposed to rank the Ophiuroidea as one of the classes of Echinoderma they were divided into two groups—the Ophiuræ and Euryalæ of Joh. Müller, the Ophiuridæ and Euryalidæ of Th. Lyman. In 1867 Dr. Axel Ljungman [7] divided the first group into six families (the Ophiodermatidæ, Ophiolepididæ, Amphiuridæ, Ophiomyxidæ, Ophiocomidæ, and Ophiothricidæ), but Mr. Lyman [10], in his description of the Ophiurids collected during the 'Challenger' Expedition, made no use of family divisions. He simply divided the Ophiuridæ into three groups, of which the first two were unnamed, and the third was merely described as comprising "Astrophyton-like Ophiuroids." Hence Lyman's great monograph, the richest mine of information in the whole range of literature on the Ophiurids, did not contribute so much to their classification as to our knowledge of their anatomy.

As neontologists were in difficulties owing to the lack of a satisfactory arrangement of the recent species, palæontologists were naturally in a worse state; for the anatomical characters of the fossil Ophiurids had been in but few cases satisfactorily determined. We have only to refer to Wright's introduction to the British Jurassic Starfish [20], or to Lütken's [9. pp. 70–75, 78] heroic attempt to improve the generic nomenclature of the Neozoic Ophiurids, to see how unscientific the existing systems were. In 1886 and 1890, Herr B. Stürtz, in two important memoirs [15, 16], described the anatomy of several genera from the Devonian of Bundenbach, in the Bavarian Pfalz. The fossils are pseudomorphs in iron pyrites; owing to the exceptional preservation of the specimens and the skill and patience with which Stürtz dissected them from their clay-slate matrix, their anatomical structure was well displayed. Stürtz's two papers are a great advance on any previous work dealing with Palæozoic Ophiurids; but the author

retained Joh. Müller's two orders, as he did also in his latest paper.

In 1892 a short and pregnant paper by Prof. F. J. Bell [1] lifted the classification of the Ophiurids on to a different plane. Bell recognized the great importance of the vertebral ossicles and that they are of three main types: (1) the "streptospondyline," where the vertebral ossicles articulate by saddle-shaped surfaces, which do not bear lateral processes or pits; (2) the "zygospondyline," where lateral processes and pits on the articular surfaces of vertebral ossicles limit the power of movement; (3) the "cladophiuroid" (or astrophiuroid), where the vertebral ossicles articulate by hourglass-shaped surfaces.

Bell therefore proposed to divide the Ophiurids into three groups: (1) the Streptophiuræ, for those with streptospondyline ossicles; (2) the Cladophiuræ, for those with hourglass-shaped articulations; (3) the Zygophiuræ, for those with zygospondyline ossicles.

The definition of these three orders was no doubt a great improvement on any previous arrangement of the Ophiurids. There is, however, considerable difficulty in applying this system to the fossil forms, especially in the case of the Streptophiuræ. It appears doubtful whether even some recent genera, as *Ophiohelus*, can be correctly described as having vertebral ossicles articulating by ball-and-socket joints. But this statement certainly cannot be made of many Palæozoic Ophiurids, which represent a more primitive condition than that of the recent species; they are indeed so primitive that they cannot be made to enter into any of Bell's orders.

The two most striking characters of these Palæozoic genera are the absence of ventral arm-plates[1] and of true vertebral ossicles. The latter are represented by free paired plates, like the ambulacral ossicles of Asterids.

The ambulacral ossicles are the most important plates in the arms of both Asterids and Ophiurids, so that it is *à priori* probable that they offer a better basis for classification than the external arm-plates. As we descend from the Zygophiuræ, first to the Cladophiuræ, and then to the Streptophiuræ, we notice a decrease in the complexity and completeness of the vertebral ossicles. It is not therefore surprising, when we go back to Palæozoic times, to find Ophiurids with an arm-structure still simpler than anything found in the Streptophiuræ. In these early forms the central arm-ossicles occur as a double series of free plates, below which is an open ambulacral groove. Hence the arms appear, at first sight, to be Asterid rather than Ophiurid in arrangement.

Hence I propose to found a fourth order of Ophiuroidea to include those without vertebral ossicles, but which have in each arm a double series of free ambulacral plates, which articulate like

[1] This character is also found in the genus *Ophioteresis* of Bell, one of the most primitive of living Ophiurids; it has, however, vertebral ossicles with streptospondyline articulations.

those of Asterids and of the Echinid *Palæodiscus*. As the two elements which have fused to form the vertebral ossicles of later Ophiurids are unattached in the members of this order, I propose for it the name Lysophiuræ[1].

No one has worked at the Palæozoic Ophiurids without being impressed by the unsatisfactory nature of many of the genera. In my earliest palæontological paper (1889) I pointed out that *Protaster* would have to be split up into more than two genera [5. p. 27]. Stürtz, both in 1890 [16. p. 245] and 1893 [17. p. 19], also insisted that *Protaster* includes a miscellaneous group of species, and that the Protasters of Forbes, Billings, Hall, and myself are distinct. I shrank from the task of dismembering this genus in 1889, as I hoped for better specimens of the type species. None such, however, have been forthcoming. As I am now bound to attempt to indicate the relations of the fossil and recent forms in an account of the Ophiuroidea for Prof. Lankester's 'Oxford Natural History,' I delay no longer. In order to simplify my task in that place, I offer the following synopsis of the classification of the Palæozoic Ophiurids, with diagnoses of some of the genera.

Order I. LYSOPHIURÆ.

Diagnosis.—Ophiuroidea of which the ambulacral ossicles are alternate and are not united into vertebral ossicles. There are no ventral arm-plates, and the underside of the arm is occupied by an ambulacral furrow.

Remarks.—This order includes a group of Palæozoic Ophiurids in which the arm-structure is on the same plan as in the Asterids; for there are no ventral arm-plates, there is an ambulacral groove, and the ambulacral plates are in double series. The members of the order differ from the Asterids by having the arms sharply marked off from the disc; while the alimentary canal was, in all probability, entirely limited to the disc.

So far as is known at present, the order was limited to the Palæozoic period; but it is necessary to consider whether a few recent forms ought not to enter it. In *Ophiohelus* and *Ophiotholia* the ambulacral plates occur as pairs of rod-like plates, instead of as vertebral ossicles. They therefore, in this respect, resemble Lysophiurids. On application to the Zoological Department of the British Museum, I find that both genera are represented only by the small single specimens dredged by the 'Challenger.' It is too great a responsibility to subject these fragile type specimens to the risk of re-examination, especially as the nature of the articular surfaces could not be determined without dissection. Both specimens are so small, that, as Prof. Bell suggests, it is quite possible they are not mature.

The members of the two genera, however, differ from the Palæozoic Lysophiuræ in three respects: they have the ambulacral

[1] From λύσις, dissolution, unattachment.

plates opposite one another; they have dorsal and ventral arm-plates; they have no ambulacral groove. To include these genera among the Lysophiuræ would limit the diagnosis of that order to the single character of the unfused nature of the ambulacral plates.

It is therefore advisable to retain *Ophiohelus* and *Ophiotholia* among the Streptophiuræ and attribute the character of their ambulacral plates either to immaturity or degeneration. Support to this conclusion is given by the fact that even among the Zygophiuræ the ambulacral ossicles begin as pairs of simple free bars (Ludwig, 8. Bd. ii. p. 94, pl. x. figs. 2–5).

Family 1. Protasteridæ.

Diagnosis.—Lysophiuræ which have boot-shaped ambulacral ossicles. Each of them consists of a "body" lying beside the middle line of the arm, and of a lateral "wing" projecting transversely from the body of the ossicle.

Genus 1. Protaster, Forbes, 1849 [4. pl. iv.].

Synonyms:

Protaster, Hall.

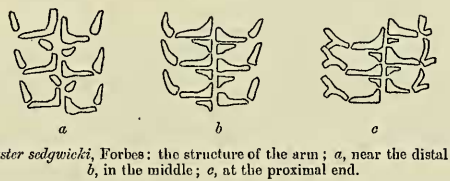
Protaster pars of Salter, Billings, Miller, Gregory, Stürtz.

Non *Protaster* of Meek and Worthen, Dewalque, Davy.

Diagnosis.—Protasteridæ with a well-marked disc; long, tapering, very flexible arms. Some of the adambulacral ossicles are Y-shaped. Scales of the disc fairly large.

Type species.—*Protaster sedgwicki*, Forbes, 1849. Silurian, Westmoreland. (Fig. 1 *a*, *b*, *c*.)

Fig. 1.



a *b* *c*

Protaster sedgwicki, Forbes: the structure of the arm; *a*, near the distal end; *b*, in the middle; *c*, at the proximal end.

Remarks.—This genus was founded by Forbes on specimens from the Ludlow rocks of Kendal, Westmoreland, which are in the Cambridge Museum[1]. Forbes's figures of the arm-structure are not satisfactory, and the accompanying diagrams will help to explain it.

[1] I must express my thanks to Prof. T. McKenny Hughes and Mr. H. Woods for facilities in examining the type. I am indebted to Mr. E. T. Newton and Mr. H. Allen for the opportunity of seeing the actual mould which was studied by Forbes, and also for that of describing the following species.

Forbes's figure represents the ambulacral ossicles as being alternately large and small. It is quite possible that each small pair represents a segment, and that the smaller ossicles have been reduced by absorption in order to give space for the podia. This explanation, however, seems improbable; for in that case there would be only one podion, instead of a pair, to each segment. The correct explanation appears to be that the smaller pieces are only triangular, distal portions of the ambulacral ossicles, apparently separated from the proximal portion by a groove. The ambulacral plates of *Cheiroptaster giganteus*, Stürtz [16. pl. xxx.], for example, are forked, and the junction is depressed; if we only knew this genus from internal casts, it would appear that the two prongs of the forked piece were separate. Many old figures represent Palæozoic Ophiurids as having the ambulacral ossicles alternately large and small; but it is quite possible that the explanation suggested will account for all such cases.

PROTASTER BIFORIS [1], n. sp. (Figs. 2, 3, p. 1033.)

Diagnosis.—Disc fairly large; interbrachial outlines concave. The syngnaths [2] are simple, prominent, and stout. The ambulacral ossicles consist of a thick body and a stout curved wing. The distal margin of the ossicles is notched by a depression for a ventral muscle-field, which also cuts into the proximal margin of the adjoining ossicle. Owing to these muscular depressions the arm has apparently two series of pores.

The adambulacral ossicles are massive and taper slightly to their distal ends; they are closely attached and form a regular series of marginal plates.

Arms very flexible.

Dimensions:

Length of longest arm	18	mm. + *x*.
Diameter of arm at the base	2·5	„
„ arm near the distal end	1	„
„ mouth	1·5	„
Length of syngnath	1	„
Width of ambulacral furrow at edge of disc.	1·25	„

Distribution.—Wenlock Shale. Castell Dinas, Bran, near Llangollen. Mus. Pract. Geol. No. VI. $\frac{6}{11}$.

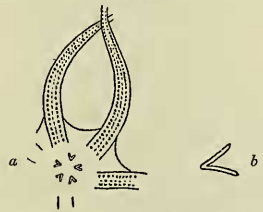
Affinities.—This species of *Protaster* differs from *P. sedgwicki*, Forbes, in having concave interbrachial outlines and roughly triangular adambulacral ossicles, and also by the character of the ambulacral ossicles. The species is of interest as showing that the flexibility of the arms is due to the great development of some ventral inter-ambulacral muscles. Thereby the arms could be rolled up ventrally and the ambulacral furrow thus protected.

[1] *Biforis*, having two holes or openings; a character due to the hole-like appearance of the ventral muscle-pits.

[2] "Syngnath," the united piece formed of mouth-frame and jaw. The "Mundecksteck."

This new species differs from *Protaster forbesi*, Hall [No. 6. pp. 293–294, pl. ix. figs. 5, 6], by the interbrachial margins of the disc being concave: in *P. forbesi*, moreover, the adambulacral ossicles are free distally, and each bears a single large spine: the ambulacral ossicles of the two species are also differently shaped.

Fig. 2.



Protaster biforis: *a*, outline of the disc and arms; *b*, a pair of syngnaths.

Fig. 3.

Protaster biforis: diagram of the arm-structure.

It was suggested in the description of *P. sedgwicki* that the apparent alternation of large and small ambulacral ossicles in that species and some other genera was probably due to a series of depressions across the ossicles. The present species suggests a possible explanation of the nature of those depressions, for they probably had the same function as the deep pits in the ossicles of the new species; and these, in all probability, were for the lodgment of the ventral muscles which moved the arms.

Genus 2. Bundenbachia, Stürtz, 1886 [15. p. 83].

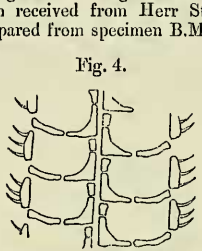
Diagnosis.—Disc soft and delicate; covering-plates apparently small and thin. Ambulacral ossicles with a dumbbell-shaped body and thin tapering wing. The body of the ossicle is apparently divided into two pieces by a transverse depression. The adambulacral plates are small and narrow, and support a triangular spine-bearing plate.

The syngnaths are curved, narrow bars.

Type species.—*Bundenbachia beneckei*, Stürtz.

Remarks.—The diagnosis of this genus is based on specimens in the British Museum received from Herr Stürtz. The diagram (fig. 4) has been prepared from specimen B.M. No. E 3495.

Fig. 4.



Bundenbachia: arm-structure.

Bundenbachia differs from *Protaster* by the irregular nature and soft plating of the disc, by the presence of spine-bearing plates attached to the adambulacral ossicles, and by the different form of the ambulacral ossicles.

Family 2. Palæophiuridæ.

Diagnosis.—Lysophiuræ in which the ambulacral ossicles are long and bar-shaped, with the longer axis parallel to the arm.

Remarks.—This family agrees with the Protasteridæ in not having the ambulacral ossicles of each segment placed opposite one another. It differs by having the ambulacral ossicles longer than wide, and never divided transversely by muscular depressions. The ambulacral ossicles are either bar-shaped or thickened to a subquadrate form. They are never boot-shaped.

Genus 1. Palæophiura, Stürtz, 1890 [16. p. 233].

Diagnosis.—Palæophiuridæ with the disc surrounded by rod-shaped marginal ossicles. The ambulacral ossicles are rods lying parallel to the arm.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Palæophiura simplex*, Stürtz.

Genus 2. Sturtzura, nov. gen.

Diagnosis.—Palæophiuridæ having thick, subquadrate, ambulacral ossicles and narrow adambulacral plates. The disc is fragile, and its plates are small and thin: it has no marginal plates. The mouth-frames are narrow and separate.

Distribution.—Silurian, England and Australia.

Type species.—*Sturtzura brisingoides* (Gregory), 1889 [5].

Remarks.—This genus differs from *Palæophiura*, as the ambulacral ossicles are thick and subquadrate, instead of being in the

form of narrow bars; also by the absence of the strong marginal plates round the disc. The genus contains two species, *S. brisingoides* (Greg.) and *S. leptosoma* (Salt.) [13. p. 331, pl. ix. fig. 5], both of which were originally placed in *Protaster*.

The genus differs from *Protaster* by the family character of having bar-shaped instead of boot-shaped ambulacral ossicles.

I have pleasure in naming this genus after Herr Stürtz, whose careful dissections have added so greatly to our knowledge of the Palæozoic Ophiurids, and who has previously pointed out [17] that these two species are generically distinct from *Protaster*.

Genus 3. Tæniura, nov. gen.

Diagnosis.—Palæophiuridæ with a small pentagonal disc, not bounded by marginal ossicles. The ambulacral furrow is broad. The oral skeleton is conspicuous and the syngnaths each composed of two separate pieces. The two jaws of each oral angle are closely attached; the mouth-frames are separated and each of them is a short, thick, slightly bent bar.

Distribution.—Trenton Limestone, Ottawa.

Type species.—*Tæniura cylindricus* (Billings) [2. pp. 81–82, pl. x. figs. 4 *a*, 4 *b*].

Remarks.—This genus differs from *Palæophiura* by the absence of marginal ossicles from the disc, and from *Sturtzura* by the smaller size of the disc and the form of the syngnaths. In *Sturtzura* the jaws end bluntly against a jaw-plate, whereas in *Tæniura* they appear to taper to a point and have no jaw-plate.

This genus is necessary for the second species included by Billings in his genus *Tæniaster*. The genus was described as discless, which in respect to the type species *S. spinosus* is correct. In that species the oral skeleton consists of five pairs of large adambulacrals as in ordinary Asterids. The affinities of the true *Tæniaster* appear to me to be with such forms as *Palæaster ruthveni* (Forbes) [4. dec. 1, pl. i. fig. 1]. It is asteroid in the oral armature, in its alternately arranged ambulacral ossicles [1], and in the absence of a disc. I therefore consider *Tæniaster* a genus of Asteroidea. The second species placed by Billings in this genus has, however, a well-marked disc [2], and has the oral armature composed of five pairs of Ophiuroid syngnaths. It must therefore be included among the Ophiuroidea.

Genus 4. Eugaster, Hall, 1867 [6. p. 290, pl. ix. figs. 7, 8].

Diagnosis.—Palæophiuridæ in which the ambulacral ossicles are subheptagonal in form, the central suture along the arm being zigzag, while the outer angles of the ossicles are cut away for the

[1] Billings in his description (2, p. 81) attributes the alternation of the ossicles in *Tæniaster spinosus* to distortion; but this explanation is not consistent with his figure. If distortion had separated the pairs of ambulacral ossicles it ought also to have displaced the syngnaths; but those of each pair are left precisely opposite.

[2] Billings, *op. cit.* pl. x. fig. 4 *a*.

reception of the podia. The adambulacral ossicles have a flat base, and thence bend forward crescentically. The mouth-frames are massive, and those of each pair meet along the middle line of the oral angle.

Distribution.—Hamilton Series, Middle Devonian, Madeson County, New York.

Type species.—*Eugaster logani*, Hall.

Remarks.—This genus I only know from Prof. Jas. Hall's figures, and in spite of their clearness I feel much doubt as to the wisdom of diagnosing it from these alone. Its affinities are clearly with the Palæophiuridæ, but it approaches the Protasteridæ in one respect: for, owing to the deep depressions in the outer angles of the ambulacral ossicles, the outer side forms a short rudimentary wing. The genus differs from all the Protasteridæ by the absence of a muscular groove across the ambulacral ossicles.

Among the Palæophiuridæ it differs from *Palæophiura* by the absence of marginal ossicles, and from *Sturtzura* and *Tæniura* by the massive nature of the mouth-frames.

Genus 5. Ptilonaster, Hall, 1867.

Distribution.—Chemung Series, Upper Devonian, Cortlandville, New York State.

Type species.—*Ptilonaster princeps*, Hall, 1867 [6. p. 292, pl. ix. fig. 9].

Remarks.—This genus is an ally of *Eugaster*, as Lütken [9. pt. iii. p. 82] has already remarked; it is, however, generically distinct. I only know it from Hall's figures, and therefore prefer to leave the preparation of a formal diagnosis to an American palæontologist.

Order II. STREPTOPHIURÆ, Bell, 1892.

Diagnosis.—Ophiuroida in which the ambulacral ossicles are opposite and are generally fused into vertebral ossicles. In such cases the vertebral ossicles articulate by a more or less simple ball-and-socket joint. The covering-plates of the arms are more or less regularly developed, and consist of a superior, an inferior, and a pair of lateral arm-plates to each segment. The lateral arm-plates generally bear spines.

Remarks.—The main character of this order is that the ambulacral ossicles are paired, but primitive. The order differs from the preceding by having the vertebral ossicles always opposite instead of alternate. In some of the simplest members of the order, as *Ophiurina*, the ossicles are not fused, there are no ventral arm-shields, and an ambulacral furrow runs along the ventral side of the arm. In the next higher family, as in the genus *Lapworthura*, the ambulacral ossicles are fused, but have plain articulating surfaces, and there is an ambulacral furrow. In recent members of the group the vertebral ossicles are of a more complex type, but the articulating surfaces are streptospondyline; in some, such as

Ophioteresis (Bell, 1. pp. 178–9, pl. xi. figs. 1–5), there are no ventral arm-plates, but this is very exceptional among recent members of the group.

Family 1. Ophiurinidæ.

Diagnosis.—Streptophiuræ with ambulacral ossicles, only slightly united, and without ventral arm-plates.

Genus 1. Ophiurina, Stürtz, 1890 [16. p. 232].

Diagnosis.—Disc circular, with marginal plates. Ambulacral ossicles long, narrow bars. Syngnaths rod-shaped. Adambulacral plates absent or altogether lost from the fossil.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Ophiurina lymani*, Stürtz, 1890.

Genus 2. Tremataster, Worth. & Mill. 1883.

Diagnosis.—Disc with concave interbrachial outlines. No marginal plates. Ambulacral ossicles short. Adambulacrals present.

Distribution.—Chester Limestone, Lower Carboniferous, Illinois.

Type species.—*Tremataster difficilis*, Worth. & Mill. 1883 [19. p. 330, pl. xxxi. fig. 3][1].

Family 2. Lapworthuridæ.

Diagnosis.—Streptophiuroida without ventral arm-plates or buccal shields; ambulacral ossicles fused, but their articulating surfaces are plain. Madreporite dorsal.

Genus 1. Lapworthura, nov. gen.

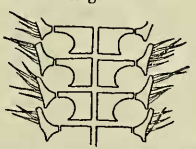
Diagnosis.—Disc circular, well-marked. Arms very flexible, broad; at first uniform in width and then tapering slowly. Ambulacral ossicles with the distal and proximal margins parallel; with lateral wings curving round the podial pores. Madreporite large.

Distribution.—Ludlow Series, Silurian, Ludlow.

Type species.—*Lapworthura miltoni* (Salter), 1857 [13. p. 330, pl. ix. fig. 4; 14].

The arm-structure is shown in fig. 5.

Fig. 5.



Lapworthura: diagram of the arm-structure, seen from ventral side.

[1] The *Protaster decheni*. Dew. (Ann. Soc. géol. Belg. vol. viii. 1880, pp. 52–54, pl. iii. figs. 1–2), is probably also a member of this genus.

Genus 2. Furcaster, Stürtz, 1886 [15. p. 79].

Diagnosis.—Disc circular small. Arms short, narrow, slightly flexible, tapering gradually. Ambulacral ossicles of a long central body and two short wings, which are attached only to the anterior corner of the ossicle.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Furcaster palæozoicus*, Stürtz[1].

Remarks.—In Stürtz's description he refers to the existence in this genus of ventral arm-plates, and even figures them. His type specimens are now in the British Museum, but I cannot verify the existence of any ventral arm-plates. His type (B.M. E 3805), for example, seems to me to show almost conclusively that an open furrow ran along the underside of the arm.

Genus 3. Palastropecten, Stürtz, 1886 [15. p. 88].

Diagnosis.—Disc circular, large (badly preserved in the specimens; probably originally soft and irregular). Arms thick, broad, and somewhat lanceolate in shape. Ambulacral ossicles narrow, the lateral wings resting on the whole body of the ossicle.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Palastropecten zitteli*, Stürtz, 1886 [15].

Aganaster, sp., Miller & Gurley [12. p. 57, pl. ix. figs. 10, 11], seems to me to be allied to *Lapworthura*, and at least a member of the same family. It apparently has no ventral arm-plates, but an open furrow, and thus differs widely from *Aganaster* It is probably a new genus.

Family 3. Eoluididæ.

Diagnosis.—Streptophiuræ with the ambulacral ossicles united to form vertebral ossicles. Ventral arm-plates present, but there are no buccal shields. (Dorsal arm-plates present only in the highest genus.)

Remarks.—This family includes three Devonian genera, which differ from the previous families of this order by the presence of ventral arm-plates and by having vertebral ossicles, which articulate (?always) by simple rounded pits and processes. The family differs from living Streptophiuræ by the absence of buccal shields and the simplicity of the oral armature.

Genus 1. Eoluidia, Stürtz, 1886 [15. p. 89].

Diagnosis.—Disc rather large; the interbrachial outlines are deeply concave. Each syngnath consists of pairs of mouth-frames and jaws; a jaw-plate is present. The vertebral ossicles are small and the union of the two lateral elements incomplete; the lateral

[1] The *Protaster daoulasensis*, Davy (Bull. Soc. géol. France, ser. 3, vol. xiv. pp. 182–187), is an ally of *Furcaster*.

wings are thin. The adambulacral plates are triangular and each of them bears several spines. The pores for the podia occur at the middle of the lateral margin of the ventral arm-shields.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Eoluidia decheni*, Stürtz, 1886.

Genus 2. Eospondylus, nov. gen.

Diagnosis.—Disc circular. Ambulacral ossicles completely fused into vertebral ossicles, each of which, however, is traversed by a pore. The adambulacral ossicles are somewhat pear-shaped. The podial pores are at the posterior angles of the ventral arm-plates.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Eospondylus primigenia* (Stürtz), 1886 [**15.** p. 77].

Genus 3. Miospondylus, nov. gen.

Diagnosis.—Disc circular. Ambulacral ossicles completely united; each half of the vertebral ossicle is boot-shaped. The oral angles each consist of a pair of syngnaths without jaw-plate. The ventral arm-plates are small, and are not notched by podial pores.

Distribution.—Lower Devonian, Bundenbach.

Type species.—*Miospondylus rhenanus* (Stürtz), 1893 [**17.** p. 29, pl. i. figs. 1–3].

Remarks.—The two genera *Eospondylus* and *Miospondylus* are both founded on species described by Stürtz, and included by him in *Ophiura*. It is impossible that they can remain in this genus, and Stürtz, no doubt, only placed them there provisionally. They agree in family characters with *Eoluidia*, but differ from it in the structure of both the ambulacral and adambulacral plates. The differences between them would certainly rank as of generic value among recent Ophiurids. To leave the two species in *Eoluidia* would only encourage the neglect of specific characters and a looseness of description which has already greatly retarded the study of the fossil Ophiurids.

Genus 4. Aganaster, Miller & Gurley, 1890.

Syn. *Ophiopege*, Böhm.

This genus was proposed by its authors to include a species described as *Protaster gregarius* by Worthen and Meek. It has nothing to do with *Protaster* and is clearly a member of the Streptophiuræ. As far as its characters are known to me it must be included among the Eoluididæ. It differs from the rest of this family by the presence of dorsal arm-plates.

Without the opportunity for the examination of more specimens than there are in the British Museum, I do not care to attempt a new diagnosis. Improvements on the original diagnosis of Miller and Gurley must be left to American palæontologists.

Böhm has founded the genus *Ophiopege* on the type species of *Aganaster* [2 *a*. p. 159].

The genus *Cholaster* of Worthen and Miller [19. pp. 328–329, pl. xxxi. fig. 4] appears to be allied to *Aganaster*, but the structure of the ambulacral ossicles is unknown.

Family 4. Onychasteridæ.

Diagnosis.—Streptophiuræ with well-developed vertebral ossicles, and with very flexible, contorted, unbranched arms; there are no external arm-plates, the integument containing granules only.

Distribution.—Keokuk and Burlington Stages, Lower Carboniferous, Iowa and Illinois.

Genus Onychaster, Meek & Worth.

Type species.—*Onychaster flexilis*, Meek & Worth. [Proc. Acad. Nat. Sci. Phil. 1869, p. 83; 11. pp. 526–528; 11 *a*. p. 510, pl. xvi. fig. 3].

Remarks.—This interesting genus has hitherto been placed among the Euryalidæ, of which it has been regarded as the best known fossil representative. As Prof. Bell, however, has remarked, Meek and Worthen's clear figures of the vertebral ossicles show that the articular surfaces are Streptospondyline and not Cladiophiuroid.

Family 5. Eucladiidæ.

Diagnosis.—Streptophiuræ with contorted branching arms. There are five pairs of large plates (? radial shields) on the abactinal side. The madreporite is large and dorsal in position. The arms have no external arm-plates, but are covered by a granular integument. Ambulacral ossicles primitively Streptospondyline.

Genus Eucladia, H. Woodward, 1869 [18].

Type species.—*Eucladia johnsoni*, H. Woodward, Lower Ludlow, near Dudley.

Remarks.—The affinities of this magnificent Starfish have been left in some doubt owing to the absence of information as to the structure of the vertebral ossicles. It has generally been assigned to the Euryalidæ, owing to its granular integument and branching contorted arms. Fortunately, however, I have found the articular surface of the vertebral ossicles exposed on the side of the block of limestone containing the specimen. The articulation is truly Streptospondyline of a rather primitive type (fig. 6 *a*, *b*, p. 1041). The ossicle is egg-shaped in section, with the broader end above. Two broad muscle-fields occur, one at each of the quadrants of the ossicle. On the central line just above these there is a small knob. The upper half of the ossicle is occupied by two pairs of depressions separated by simple ridges.

The structure is on essentially the same plan as that of *Onychaster* and it is clearly Streptospondyline in character. The genus

Fig. 6.

a *b*

a & *b*, articular surfaces of the vertebral ossicles of *Eucladia*. $\frac{1}{1}$.

is therefore to be included among the Streptophiuræ, the resemblances to the Euryalidæ being homoplastic modifications to suit its mode of life.

The Homologies of the Madreporite.

The madreporite in *Eucladia* is certainly dorsal, as Dr. Woodward correctly stated; it has been suggested that this character removes the genus from the Ophiuroidea. In that case *Lapworthura* and probably *Protaster* will also have to be excluded from this subclass. But in most Echinoderms the water vascular aperture opens on the aboral surface. According to Bury [2 *b*. pl. xxxvii. fig. 2, pp. 422–423], the water-pore of the Ophiuroidea originally occupies this position. It is therefore not unreasonable to suppose that in the earliest Ophiurids the water-pore was originally dorsal, and that it subsequently worked round to the ventral side, as it does during the development of the Spatangoida. Hence one cannot use the dorsal position of the madreporite in Palæozoic Stellerids as a proof that they are not Ophiurids.

It follows from this, however, that the madreporite (or plate in which the water-pore opens) of *Lapworthura* and *Eucladia* is not homologous with the madreporite of recent Ophiurids, which belongs ontogenetically to the oral system. Carpenter and Bury have both adduced strong reasons to show that the madreporite of Ophiurids is not homologous with that of Asterids. The evidence of the Palæozoic genera of both groups shows that this plate is not homologous in all the members of even the same subclass. It is certain that in some Ophiurids the madreporite is oral, and that in others it is not. Hence it is quite possible that in those Asterids with a ventral madreporite, the plate may be a member of the oral system.

Although, therefore, the madreporite may originate ontogenetically on an oral, it does not do so phylogenetically, and the situation of the water-pore on an oral plate has resulted only from a secondary modification,

Synopsis of Classification.

Class **STELLEROIDA.**

Subclass OPHIUROIDEA.

Order I. **Lysophiuræ.**—Ambulacral ossicles alternate, free. No ventral arm-plates.

Fam. 1. PROTASTERIDÆ. Boot-shaped ambulacral ossicles.
Genera.—*Protaster*, Forbes.
Bundenbachia, Stürtz.

Fam. 2. PALÆOPHIURIDÆ. Long bar-shaped ambulacral ossicles.
Genera.—*Sturtzura*, Greg.
Palæophiura, Stürtz.
Tæniura, Greg.
Eugaster, Hall.
Ptilonaster, Hall.

Order II. **Streptophiuræ.** Vertebral ossicles present, with more or less Streptospondyline articulations

Fam. 1. OPHIURINIDÆ. Ambulacral ossicles slightly united and no ventral arm-plates.
Genera.—*Ophiurina*, Stürtz.
Tremataster, Worth. & Mill.

Fam. 2. LAPWORTHIURIDÆ. Ambulacral ossicles fused. No ventral arm-plates. Madreporite dorsal.
Genera.—*Lapworthura*, Greg.
Furcaster, Stürtz.
Palastropecten, Stürtz.

Fam. 3. EOLUIDIDÆ. Vertebral ossicles. Ventral arm-plates, but no buccal shields.
Genera.—*Eoluidia*, Stürtz.
Eospondylus, Greg.
Miospondylus, Greg.
Aganaster, Mill. & Gurl.
Cholaster, Worth. & Mill.

Fam. 4. ONYCHASTERIDÆ. Contorted unbranched arms. Integument granular.
Genus.—*Onychaster*, Meek & Worth.

Fam. 5. EUCLADIDÆ. Contorted branched arms. Integument granular.
Genus.—*Eucladia*, H. Woodw.

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